Small and large wetland fragments are equally suited breeding sites for a ground-nesting passerine

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Small and large wetland fragments are equally suited breeding sites for a ground-nesting passerine

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Abstract Large habitat fragments are generally thought to host more species and to offer more diverse and/or better quality habitats than small fragments. However, the importance of small fragments for population dynamics in general and for reproductive performance in particular is highly controversial. Using an information-theoretic approach, we examined reproductive performance and probability of local recruitment of color-banded reed buntings *Emberiza schoeniclus* in relation to the size of 18 wetland fragments in northeastern Switzerland over 4 years. We also investigated if reproductive performance and recruitment probability were density-dependent. None of the four measures of reproductive performance (laying date, nest failure probability, fledgling production per territory, fledgling condition) nor recruitment probability were found to be related to wetland fragment size. In terms of fledgling production, however, fragment size interacted with year, indicating that small fragments were better reproductive grounds in some years than large fragments. Reproductive performance and recruitment probability were not density-dependent. Our results suggest that small fragments are equally suited as breeding grounds for the reed bunting as large fragments and should therefore be managed to provide a habitat for this and other specialists occurring in the same habitat. Moreover, large fragments may represent sinks in specific years because a substantial percentage of all breeding pairs in our study area breed in large fragments, and reproductive failure in these fragments due to the regularly occurring floods may have a much stronger impact on regional population dynamics than comparable events in small fragments.

Keywords Akaike's information criterion · Avian reproductive performance · Fragmentation · Recruitment probability · Spatially structured populations

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Introduction

Large habitat fragments are generally considered to be superior habitats for many plant and animal species compared to small fragments. Recent reviews suggest that large fragments may host more species, offer more diverse habitats and have higher quality interior habitats and relatively less edge habitat than small fragments (Harrison and Bruna 1999; Debinski and Holt 2000; Laurance et al. 2002; Fahrig 2003). However, these reviews also point out that responses of species and communities to habitat loss and fragmentation are highly variable and not necessarily negative. Similarly, Fischer and Lindenmayer (2002) showed that small fragments (<1 ha) may be valuable as well because such fragments hosted considerable numbers of bird species, and the vast majority of species were not confined to large fragments (up to 98 ha).

While small fragments can have positive effects on species richness, their role in the dynamics of populations is controversial. For example, the reproductive performance of plant and animal species has often been found to be

lower in small fragments than large ones (Burke and Nol 2000; Luck 2003; Diaz et al. 2005; Kolb 2005), but the generality of this finding is far from clear (Wolff et al. 1997; Nour et al. 1998; Tewksbury et al. 1998; Zanette 2000; Brooker and Brooker 2001; Cooper et al. 2002). The relation between fragment size and reproductive performance may be community-specific—that is, whether or not reproduction is affected by fragment size may depend on the specific habitats and species involved. To date, most studies examining relations between fragment size and reproduction in birds have been conducted in forested or agricultural habitats. Other fragmented habitats, for example wetlands, have received comparatively little attention. This is surprising, given that wetlands throughout the world have been destroyed on a large scale, resulting in a highly fragmented distribution of the remaining wetland habitats (e.g. Hanski 2005). Whether patterns reported from forest fragments also apply to wetland fragments is unclear.

Here we present data from a 4-year study on reed buntings *Emberiza schoeniclus* (Linnaeus, 1758) conducted in 18 wetland fragments of variable size in the Swiss lowlands. Specifically, we examined whether reproductive performance, based on assessments of laying date, probability of nest failure, fledgling production and condition, and the recruitment probability of locally born individuals were related to fragment size. We further explored if reproductive performance and recruitment probability were related to local population density, given the striking importance of density dependence for demographic traits and population regulation in a variety of taxa (e.g. Sibly et al. 2005). In addition, the relations of reproductive performance or recruitment probability with fragment size and population density, respectively, have seldom been jointly addressed. The reed bunting is ideally suited for such a study because in Switzerland, this species is confined to wetlands with old reed *Phragmites* sp., and such wetlands show a highly fragmented distribution owing to severe habitat destruction over the past two centuries. Because nest predation rates are negatively associated with the distance of a nest to the reed edge (Pasinelli and Schiegg 2006) and small fragments contain smaller patches with relatively more edge habitat than large fragments (unpublished data, G. Pasinelli), we expected the reproductive performance and recruitment probability of reed buntings to be higher in large fragments than in small ones. In addition, we expected reproductive performance and recruitment probability to decline with increasing local population density, a pattern commonly observed in many animal populations (e.g. Newton 1998). Knowledge about the importance of small versus large wetland fragments can help conservation agencies guide their management actions in times of limited funding.

Methods

Study species

The reed bunting (*Emberiza schoeniclus*) is a socially, but not genetically monogamous (Dixon et al. 1994), ground-nesting passerine with a transpalearctic distribution. Individuals from Central Europe are migratory and overwinter mostly in southern and southeastern France (Glutz von Blotzheim and Bauer 1997). Large-scale population density averages eight to ten breeding pairs per 10 ha in continuous wetlands, but may be much lower in fragmented landscapes, depending on the distribution and the size of the wetlands (Glutz von Blotzheim and Bauer 1997). The presence of old reed *Phragmites* sp. is the most important cue for territory establishment when males return from the wintering grounds (Surmacki 2004). If old reed habitat is missing, reed buntings will not settle, and the respective wetland will remain unoccupied throughout the breeding season (authors' personal observations). Reed buntings defend nesting territories, which may range in size from 96 to 7500 m^2. Nests are usually placed in tussocks, heaps of old grass or under broken, horizontal old reed stems within old reed habitat, but as the breeding season progresses, nests are also placed along ditches or in sedge meadows adjacent to old reed patches (35% of the 416 nests in this study). In Central Europe, up to five breeding attempts per season can be observed, but more than two successful nests are rare. Clutch size ranges from two to six eggs and generally declines with advancing season. Nesting success is highly variable and is strongly affected by both predation and the occurrence of floods (all details from Glutz von Blotzheim and Bauer 1997). Foraging takes place in wetland vegetation outside nest territories, i.e. in undefended areas adjacent to the territory. Radio-tracking has revealed that reed buntings do not leave wetlands while foraging, a result independent of wetland fragment size (Silvestri 2006).

Study fragments

From 2002 to 2005, we recorded reproductive performance of reed buntings in 21 wetland nature reserves scattered over an area of 200 km^2 in southeastern Canton Zurich, Switzerland. These 21 nature reserves represent all of the fragments potentially suitable for reed buntings in the 200-km^2 area. All fragments are mown in autumn to prevent overgrowth with reed. Only small bands of reed along water bodies as well as a few distinct reed patches are spared from the annual cut in both the large and small fragments (see below), while large patches of old reed habitat away from the lakefront are missing. The landscape surrounding the fragments is very similar and consists mostly of agricultural lands.

We excluded two fragments that remained unoccupied in all of the study years due to an almost complete lack of old reed habitat as well as a third one with only one breeding attempt in the 4 years, resulting in data from 18 fragments. The fragments ranged in size from 1.9 to 247.2 ha (median 10.5 ha, interquartile range 4.2–16.7 ha), and the size of patches consisting of old reed (≥1 year old) within fragments varied between 0 and 2.58 ha [see Table S1 in Electronic Supplementary Material (ESM)]. Twenty to sixty pairs of reed buntings bred annually in the three largest fragments (Orniplan, unpublished report, and G. Pasinelli, unpublished data), but it would not have been feasible to monitor all of these pairs. Therefore, in each of these three large fragments, we monitored the reproductive performance of at least ten breeding pairs annually in an area of old reed along the lakefront that had been randomly selected at the beginning of the study in 2002. The same old reed areas were monitored in all years. Note that these areas of old reed along the lakes are considered to be the optimal habitat for reed buntings in that they provide both suitable nest sites and relatively dense cover with the presence of sedges and reed stems (Glutz von Blotzheim and Bauer 1997). In the other 15 fragments, all breeding pairs present were monitored annually, with the number of breeding pairs ranging from zero to five. The number of breeding pairs was highly correlated to the area of old reed (Pearson correlation $r > 0.75$ in each year, $n = 18$).

Field procedures

From mid-March to early August each year between 2002 and 2005, each study fragment was visited at least twice per week by two observers. We located nests by standing on ladders and observing females building the nest, leaving the nest and returning to it during incubation or when the parents were feeding the young. Of the 416 nests identified, 91.3% (378) were found in the egg stage. The number of eggs and/or nestlings was recorded at each visit, with intervals between subsequent nest checks of 2–4 days. If the exact hatch date was not known, nestling age was determined based on the stage of feather growth following Blümel (1995). The young were banded between nestling day 6 and 9, with each nestling obtaining an individual combination of one aluminum and three color rings. Nests were considered successful when at least one nestling reached the banding age. When ringing the young we measured the following morphological traits of each nestling: length of right tarsus (to the nearest 0.01 mm), body mass (0.25 g) and length of right wing (0.5 mm). Given that partial brood loss is rare in the nestling stage (18 of 296 nests, unpublished data, G. Pasinelli), we considered the number of nestlings banded as equal to the number of fledglings. Since the young fledge after day 9 (Glutz von Blotzheim and Bauer 1997), nests were not checked after the young had been banded to avoid premature fledging. After fledging or nest loss, nest locations were recorded using a hand-held global position system (GPS) receiver (GPS-12XL with RXMAR decoder, Garmin, Olathe, KS; GeoExplorer 3, Trimble, Sunnyvale CA; Leica GS50, Leica, St. Gallen, Switzerland). The precision of the GPS locations after differential correction was ≤2 m.

Adults were caught with mist nets using playback tapes (males) or at the nest when feeding the young (males and females). After capture, birds were individually banded with one aluminum and three color rings, and standard morphological measurements were taken. Over 90% of the study population was color banded in all study years.

From May to July 2003–2006, we systematically searched for banded birds outside the monitored old reed areas of the three large fragments and opportunistically in wetlands outside of our 200-km^2 study area. We focused our search for banded reed buntings on wetlands because the species does not use habitats other than wetlands during breeding time in the Canton Zurich. The period between May and July corresponds to the breeding season of the reed bunting in our study area; individuals observed during that time are considered territorial breeding birds. Non-breeding territorial individuals were extremely rare (unpublished data, G. Pasinelli).

Measures of reproductive performance

Laying date

We considered laying date of first broods only because the onset of subsequent clutches largely depends on whether the first nest has been successful or not. Laying date was determined either by backdating from the hatching date based on clutch size and an average incubation time of 13 days or, when a clutch was incomplete and found completed on a subsequent visit, calculated based on the final clutch size and the fact that one egg per day is laid (Blümel 1995). We excluded clutches which failed before hatching if they were seen only once in the egg stage or were found to be complete (seen at least twice in the egg stage).

Probability of nest failure

Nest failure included nests lost due to predators and to other reasons (flooding, among others). Although we were primarily interested in overall nest failure probability in relation to fragment size and local density, we also analyzed nest failure probability due to predation alone. We used the Mayfield logistic regression to model probability of nest failure and predation, respectively (Hazler 2004). A detailed description and application of this method is given

in Pasinelli and Schiegg (2006). Mayfield logistic regression assumes the probability of nest failure to be constant over time (Hazler 2004). We therefore tested whether the probability of nest failure was related to nest stage (categorical variable: egg or nestling stage), year (categorical variable: 2002–2005) and/or breeding attempt (categorical variable: 1–5). The latter variable was included because the probability of nest failure may change over the breeding season. We included a repeated term to account for more than one observation of the same nest (i.e. a nest failed in the nestling stage appears as successful in the egg stage; successful nests appear as not failed in both stages). We found that only nest stage significantly influenced the probability of nest failure ($F = 6.4$, $P < 0.02$, $n = 657$), with nests being more likely to fail in the egg stage than in the nestling stage. Hence, subsequent analyses of the effect of fragment size on the probability of nest failure were performed for the egg and nestling stage separately.

We have previously shown that nest success is influenced by nest habitat quality (Pasinelli and Schiegg 2006). Differences in nest habitat quality across sites may thus impair our ability to find relationships between nest success, fragment size and/or local density. We therefore first tested whether nest habitat quality depended on fragment size using linear mixed models (Proc Mixed in SAS Institute 2002–2003), which included as random factors both fragment identity and territory identity nested within fragments to account for multiple observations from each fragment (i.e. territories) and territory (i.e. nests), respectively. The dependent variables reflecting nest habitat quality were nest height above the ground, vegetation height above the nest, vegetation cover around the nest and the distance of a nest to the water edge (for descriptions of these variables, see Pasinelli and Schiegg 2006). The independent variable was $\log_{10}$-transformed fragment size. None of the nest habitat quality variables was related to fragment size (all $P > 0.12$); consequently, we did not include habitat quality variables in our analyses of nest failure probability.

Number of fledglings

We calculated the total number of fledglings produced per territory per year. In these analyses, we only included territories from which the total number of fledglings produced was exactly known (201 of 219 territories).

Fledgling body condition

Body mass, tarsus length and wing length of fledglings were highly correlated ($r > 0.72$, $P < 0.001$, $n = 755$ in all cases). The three morphological variables were therefore subjected to a factor analysis (Proc Factor, SAS Institute 2002–2003), which reduced them to one factor explaining 84.1% of the variation in the morphological variables. Factor loadings were larger than 0.89 for each variable. We were interested in body condition of the smallest fledgling per brood (hereafter termed "poorest fledgling") and in mean fledgling body condition per brood, respectively. Because fledglings from different nests had been banded, for example, at different times of the day and by different persons, we accounted for potential bias arising through these and other factors by means of regression analyses. For the poorest fledgling ($n = 174$), body condition was expressed as the residuals of a multiple regression of factor scores on age at ringing (Proc Mixed, SAS Institute 2002–2003; $F_{age} = 205.4$, $df = 1$, $P < 0.001$), number of siblings ($F_{sibs} = 14.7$, $df = 1$, $P < 0.001$), breeding attempt ($F_{att} = 4.9$, $df = 1$, $P < 0.03$), time of day of ringing ($F_{time} = 5.5$, $df = 1$, $P < 0.020$) and the person measuring the fledglings (hereafter "observer"; $F_{obs} = 3.7$, $df = 6$, $P < 0.002$). Similarly, the average factor scores per brood ($n = 186$) were regressed on age at ringing ($F_{age} = 192.6$, $df = 1$, $P < 0.001$), time of day of ringing ($F_{time} = 14.0$, $df = 1$, $P < 0.001$) and observer ($F_{obs} = 1.9$, $df = 6$, $P < 0.087$), with the resulting residuals used as a measure of mean fledgling body condition per brood (number of siblings and nesting attempt were not significantly related to average factor scores per brood). Broods with only one nestling surviving to ringing age were excluded in analyses involving body condition of the poorest fledgling, but they were included in analyses of mean fledgling body condition per brood. Therefore, sample sizes vary in the respective analyses.

Recruitment probability

Recruits were defined as individuals that were born and banded in our study area and re-sighted during a subsequent breeding season. Of 56 recruits, 60.7% were found within the intensively monitored fragments and old reed areas (see above), 39.3% were found outside of them (i.e. in the not intensively monitored wetland parts of the three large fragments) and none were found outside the 200-km^2 study area. Because only four of 219 territories produced more than one recruit per year, each territory was annually classified as either producing a recruit or not. Since territories with many fledglings may be more likely to produce a recruit than territories with one or only a few fledglings, we included the number of fledglings produced per territory per year as a continuous covariate in all analyses focusing on recruitment probability (i.e. whether or not a territory produced a recruit). This enabled us to examine the influence of fragment size and local density on recruitment probability, while simultaneously accounting for differences in fledgling numbers.

Local population density

As a measure of local population density, we calculated for each territory the number of reed bunting territories within 100 m of the center of the focal territory. Territory centers were defined as the geometric mean of all nests produced per territory per season. We used this measure of local density because it reflects the influence of the neighborhood on a focal territory. In a study on reed buntings, Bouwman (2005) showed that most extra-pair fertilizations were from males residing within the next two territories of a focal female, which translated into a distance of about 100 m. Density estimates based on the number of breeding pairs per 10 ha were not used because this measure does not reflect small-scale variations in densities experienced by individual territories, but rather assumes that all breeding pairs are exposed to the same average density. Across all years and fragments, local density ranged from zero to seven territories per 100-m circle ($n = 256$). Considering fragments with at least one breeding pair annually, average local density was positively correlated to fragment size in 2003 (Spearman's $R_s = 0.58$, $P = 0.024$, $n = 15$) and 2004 ($R_s = 0.60$, $P = 0.032$, $n = 13$), but not in 2002 ($R_s = 0.40$, $P = 0.124$, $n = 16$) and 2005 ($R_s = 0.43$, $P = 0.129$, $n = 14$).

Model structure and selection

Our base model, against which the performance of all the other models was compared, included the intercept term and the categorical variable year. As covariate we added to the base model the number of fledglings produced per territory per year in the analysis of recruitment probability (see above). For each measure of reproductive performance and for recruitment probability, we then added $\log_{10}$-transformed fragment size, local density (both as continuous variables) and the interactions of these two variables with year to the base model. We further examined models containing fragment size and local density jointly, with and without the interactions of fragment size and local density, respectively, with year (see Table S2 in the ESM).

The probability of nest failure and recruitment were analyzed using generalized linear mixed models with logit link and assuming binomial error distribution (Proc Glimmix, SAS Institute 2002–2003). All the other reproductive measures were analyzed with linear mixed models (Proc Mixed, SAS Institute 2002–2003). To account for several observations (i.e. territories) from each fragment, fragment identity was always included as random factor. With the exception of the analyses of laying date, fledgling production and recruitment probability, territory identity was nested within fragments and defined as a further random factor to account for more than one observation (i.e. nest) from each territory (Singer 1998). Parameter estimates were obtained using maximum likelihood (SAS Institute 2002–2003). The data set included broods of the same individuals from different years. We treated these data as independent because breeding partners and, occasionally, territory locations as well changed between years. Model fit was explored with residual analyses.

We assessed the relative performance of the models for each reproductive trait separately with Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). The AICc values were manually calculated based on log-likelihood values derived from the SAS software release 9.1.3 (SAS Institute 2002–2003). The model with the lowest AICc value represents the best compromise between overfitting due to too many parameters and model bias due to too few parameters (Burnham and Anderson 2002). We additionally calculated Akaike model weights, which denote the likelihood that a particular model is the most reasonable one among the set of models evaluated. Weights of selected models sum up to 1 by definition, and higher weights denote better explanatory power. To account for model selection uncertainty, we averaged parameter estimates and associated standard error (SE) over the set of candidate models for each dependent variable by multiplying with the weight of the particular model and summing over the entire set of models that contained the particular parameter (Burnham and Anderson 2002).

Results

Laying date

Laying date of first eggs of first clutches ranged from April 18 to May 25 (Table S3 in the ESM). The base model including the intercept and the categorical variable year was best supported by the data (Table 1). Models including fragment size and/or local density received less support than the base model. Further, model-averaged parameter estimates for fragment size and local density were (considerably) smaller than their associated SE (Table 2), suggesting that neither variable explained the variation in laying date of first eggs of first clutches (Figs. 1, 2).

Probability of nest failure

Across years, the probability of nest failure was 50.2% for a clutch of five eggs (Table S3 in the ESM), the most common clutch size, from day of the first egg until young were 8 days old (reached banding age). Model selection revealed that in the egg stage, the base model ranked highest, while models containing either fragment size or density were less than half as well supported by the data based on Akaike weights (Table 1). Model-averaged parameter estimates for fragment size and local density were small (Table 2). In the nestling

Table 1 Results of model selection by reproductive trait. Models with ΔAICc < 2 compared to best model (with smallest AICc) are shown (for all candidate models examined, see Table S2 in the ESM) and ranked by decreasing Akaike weight per trait

Reproductive trait	Models[a]	K[b]	LogL[c]	AICc[d]	ΔAICc[e]	Weight[f]
Laying date[g] (n = 120)	Intercept, year[h]	6	−411.7	836.1	0	0.387
	Density	7	−410.9	836.7	0.7	0.279
Nest failure in egg stage (n = 416)	Intercept, year[h]	6	−404.4	821.0	0.0	0.366
	Fragment size	7	−404.2	822.7	1.7	0.158
	Fragment size, fragment size × year	10	−401.1	822.8	1.8	0.148
	Density	7	−404.3	822.8	1.9	0.145
Nest failure in nestling stage (n = 262)	Intercept, year[h]	6	−164.4	341.1	0.0	0.245
	Fragment size	7	−163.3	341.1	0.0	0.244
	Density	7	−163.5	341.5	0.4	0.197
	Fragment size, fragment size × year	10	−160.9	342.6	1.6	0.112
	Fragment size, density	8	−163.1	342.9	1.8	0.101
Fledglings produced per territory (n = 201)	Fragment size, fragment size × year	10	−491.9	1005.0	0.0	0.344
	Intercept, year[h]	6	−496.5	1005.4	0.4	0.279
Condition poorest fledgling (n = 174)	Intercept, year[h]	7	−165.2	345.0	0.0	0.483
	Density	8	−165.1	347.0	1.9	0.183
Mean fledgling condition (n = 186)	Intercept, year[h]	7	−139.8	294.2	0.0	0.519
Recruitment probability (n = 220)	Intercept, year[h], number fledglings	6	−93.3	199.0	0	0.313
	Fragment size, fragment size × year	10	−89.3	199.7	0.7	0.217
	Fragment size	7	−92.8	200.1	1.2	0.176
	Density	7	−93.2	200.9	1.9	0.120

[a] Year, Study year (categorical); density, local population density; fragment size, $\log_{10}$-transformed size of the study fragments (see Table S1 in the ESM)

[b] K, Number of parameters in model including the intercept, fixed and random effects and error term (in linear mixed models only)

[c] LogL, Maximum log-likelihood estimate from SAS software release 9.1.3 (SAS Institute 2002–2003)

[d] AICc, AIC value corrected for small sample size

[e] ΔAICc, difference in AICc to the best model,

[f] Weight, Akaike weight, indicates support of a model relative to the other models considered per reproductive trait

[g] Laying date, Laying date of first egg of first clutch

[h] Base models, whose factors and covariates are included in all models of the respective reproductive trait

Table 2 Model-averaged parameter estimates (±SE) of variables in models per reproductive trait shown in Table 1

Source	Laying date	Nest failure probability		Number of fledglings	Fledgling condition		Recruitment probability
		Egg stage	Nestling stage		Poorest	Mean	
Fragment size	0.27 ± 0.77	−0.08 ± 0.20	−0.23 ± 0.34	0.34 ± 0.56	0.00 ± 0.01	0.00 ± 0.01	0.27 ± 0.42
Fragment size × year_{2002}	−0.06 ± 0.34	0.00 ± 0.11	0.09 ± 0.23	−0.15 ± 0.46	0.00 ± 0.01	0.00 ± 0.01	0.19 ± 0.42
Fragment size × year_{2003}	−0.61 ± 1.17	0.04 ± 0.15	0.05 ± 0.17	−0.05 ± 0.37	0.00 ± 0.01	0.00 ± 0.00	−0.07 ± 0.29
Fragment size × year_{2004}	−0.13 ± 0.47	0.13 ± 0.26	0.25 ± 0.46	−0.94 ± 1.32	0.01 ± 0.02	0.00 ± 0.01	−0.47 ± 0.79
Density	0.20 ± 0.33	−0.02 ± 0.05	−0.03 ± 0.07	0.01 ± 0.05	0.00 ± 0.01	0.00 ± 0.01	−0.02 ± 0.06
Density × year_{2002}	−0.02 ± 0.05	0.01 ± 0.04	0.03 ± 0.07	0.03 ± 0.06	0.00 ± 0.01	0.00 ± 0.00	−0.01 ± 0.03
Density × year_{2003}	0.03 ± 0.08	0.01 ± 0.04	−0.02 ± 0.05	0.03 ± 0.07	0.00 ± 0.01	0.00 ± 0.00	−0.03 ± 0.06
Density × year_{2004}	−0.02 ± 0.06	0.04 ± 0.07	−0.03 ± 0.07	−0.04 ± 0.09	0.01 ± 0.02	0.00 ± 0.00	0.00 ± 0.02

Omitted are parameter estimates and SE for the categorical variable year included in all models and for the variable number of fledglings produced per territory per year included in the recruitment probability model. For sample sizes see Table 1

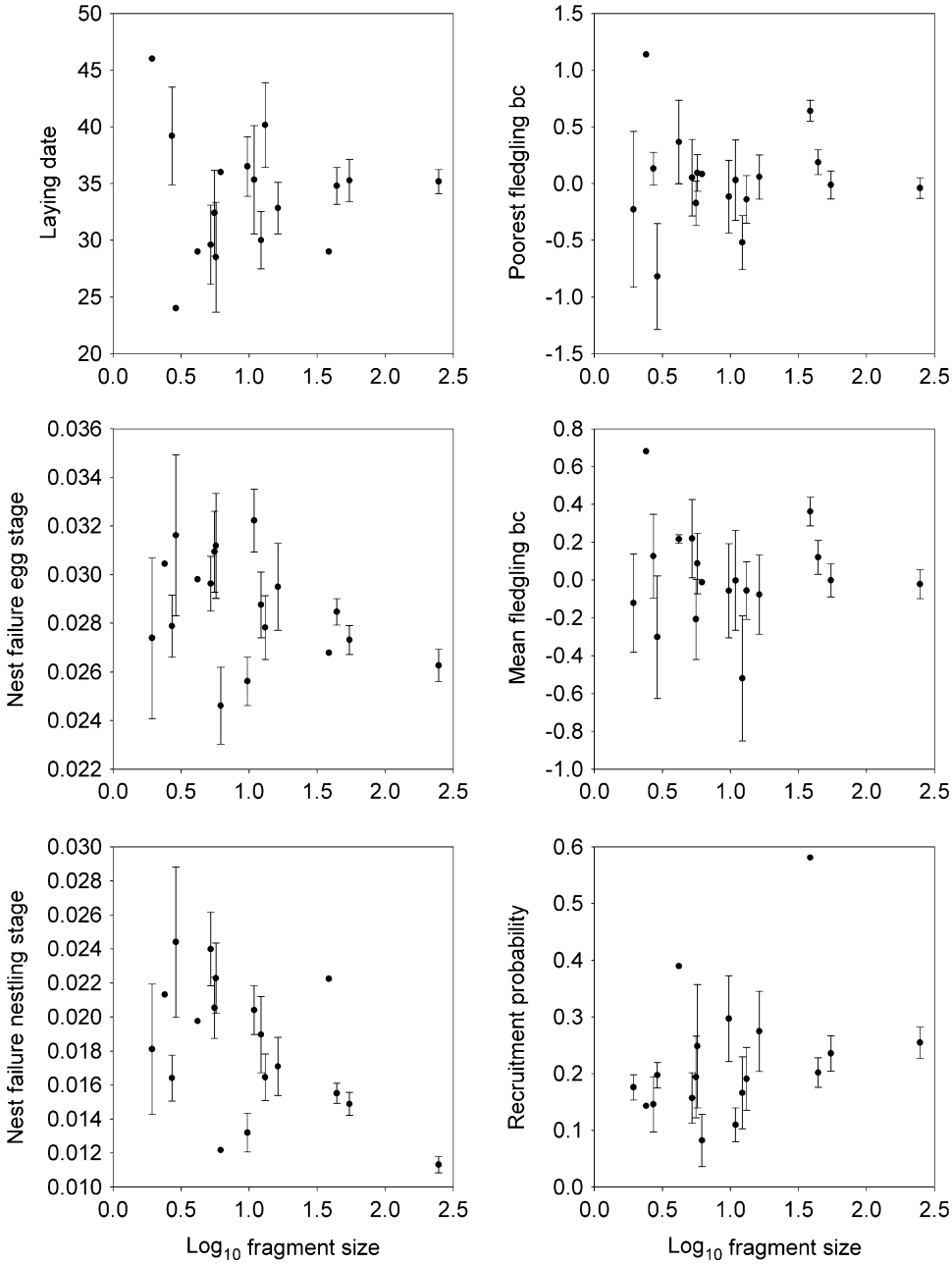

Fig. 1 Relations of fragment size with reproductive traits and with recruitment probability. Shown are mean and SE calculated per fragment size over all years. Fragment size is $\log_{10}$ of hectare values. Nest failure and recruitment probability plots show predicted values from logistic regressions with year and $\log_{10}$ fragment size as independent variables; all other plots show raw data. Laying date, Julian laying date of first eggs of first clutches; nest failure egg stage or nestling stage, daily probability of nest failure in the egg stage or nestling stage; poorest fledgling bc, body condition of the poorest fledgling per brood; mean fledgling bc, mean fledgling body condition per brood; recruitment probability, probability that a territory produced a recruit. See Methods for further details. For sample sizes, see Table S4 in the ESM

stage, the model including fragment size was equally well supported as the base model (Table 1), but the small difference (0.02) in the log-likelihood values between the two highest-ranking models suggests that the inclusion of fragment size did not substantially improve model performance (Burnham and Anderson 2002). Moreover, the model-averaged parameter estimate for fragment size was smaller than the associated SE (Table 2). Models with local density had generally less support than the base model. In summary, there was little evidence for effects of fragment size or local density on nest failure probability in either stage (Figs. 1, 2).

The same picture emerged when nest failure probability due to predation alone was examined. In the egg stage, the best-supported model was the base model, with all other models having ΔAICc to this model larger than 2. In the nestling stage, the model including fragment size ranked highest, but ΔAICc to the base model was only 1.5, and the model-averaged parameter estimate for fragment size was smaller than the associated SE (-0.43 ± 0.46, $n = 248$ nests), indicating little influence of fragment size on nest predation probability.

Number of fledglings

Overall numbers of fledglings produced per territory per year ranged from 0 to 12 and averaged 3.65 fledglings (SD = 2.85,

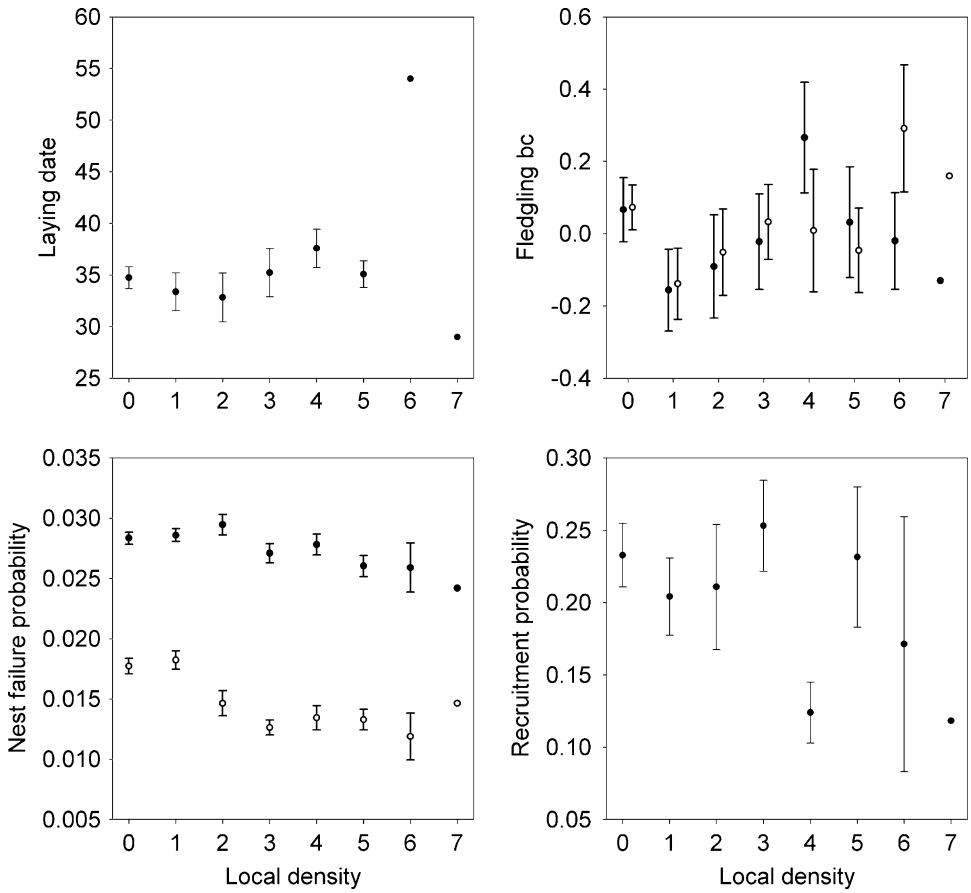

Fig. 2 Relations of fragment size with reproductive traits and with recruitment probability. Shown are mean and SE calculated per local density over all years. Local density is the number of reed bunting territories within 100 m of the center of the focal territory. Nest failure and recruitment probability plots show predicted values from logistic regressions with year and local density as independent variables; all other plots show raw data. Laying date, Julian laying date of first eggs of first clutches; nest failure probability, daily probability of nest failure in the egg stage (*filled circles*) or nestling stage (*open circles*); fledgling bc, body condition of the poorest fledgling (*filled circles*) or the mean fledgling body condition (*open circles*) per brood; recruitment probability, probability that a territory produced a recruit. For sample sizes, see Table S4 in the ESM

$n = 201$ territories). Variation in the total number of fledglings produced per territory per year was best explained by a model that included fragment size and its interaction with year (Table 1), indicating that the relation between number of fledglings and fragment size varied among years. In particular, 2004 appeared to have been an exceptional year, given the low numbers of fledglings produced in large fragments in that year, while in other years, no relations between fledgling numbers and fragment size were evident (Fig. 3, Table 2). Nevertheless, ΔAICc to the second best model, which was the base model, was only 0.4. Local density, on the other hand, did not appear to influence fledgling production.

Fledgling body condition

We found no evidence of fragment size and local density influencing either body condition of the poorest fledgling or mean fledgling body condition per brood (Table 2, Figs. 1, 2). In both cases, the base models were clearly ranked the highest (Table 1).

Recruitment probability

Over the 4 years of the study, an average (±SD) of 21.3% (±18.2, $n = 219$) of the territories produced one or more recruits (Table S3 in the ESM). Models including either fragment size or local density were less well supported by the data than the base model (Table 1). This means that neither fragment size (Fig. 1) nor local density (Fig. 2) appeared to substantially influence recruitment probability, which is corroborated by the small model-averaged parameter estimates relative to the associated SE (Table 2).

Discussion

Fragment size

In many bird species, an early onset of breeding has been shown to result in increased reproductive output (Verhulst et al. 1995; Schiegg et al. 2002; Müller et al. 2005). Further, individuals generally breed earlier in high-quality than low-quality habitats (Brodmann et al. 1997; Aho et al. 1999). Accordingly, if large fragments are better habitats than small ones, birds should start to breed earlier in the former than the latter. Some studies have confirmed this pattern (e.g. Huhta and Jokimaki 2001; Loman 2003), while others have not (e.g. Matthysen and Adriaensen 1998). In our study, laying dates of reed buntings were not related to fragment size, suggesting that

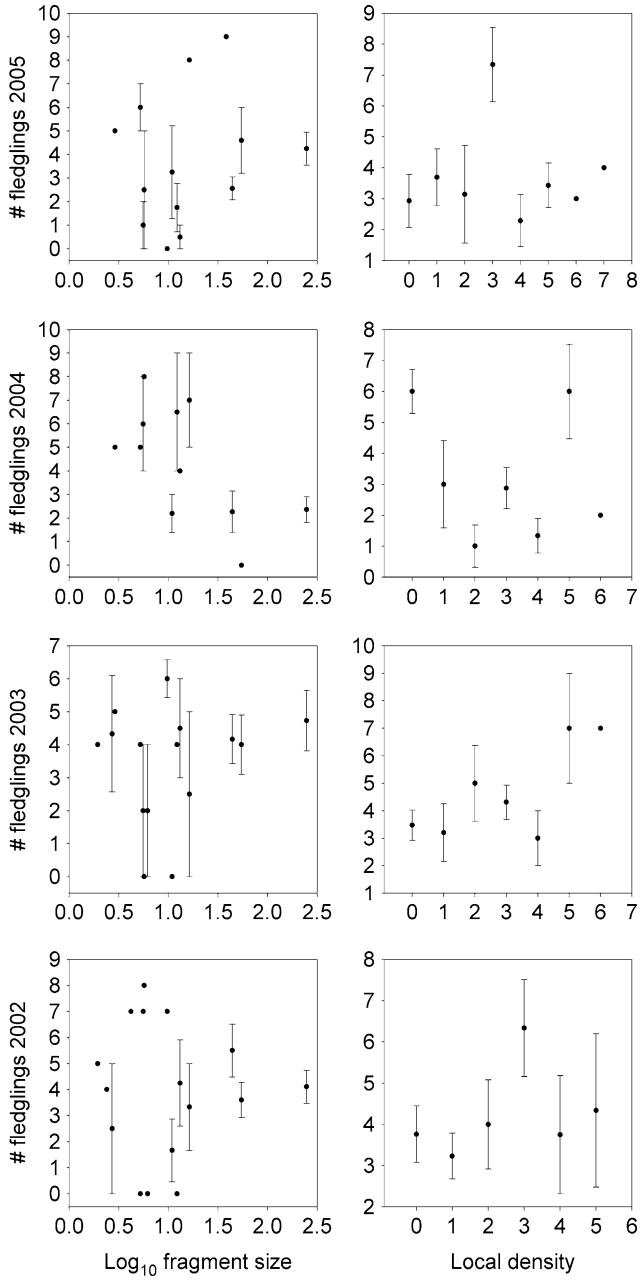

Fig. 3 Number of fledglings produced per territory and year in relation to fragment size and local density. Shown are annual mean and SE calculated per fragment size and local density, respectively. Fragment size is $\log_{10}$ of hectare values, and local density is the number of reed bunting territories within 100 m of the center of the focal territory. For sample sizes, see Table S5 in the ESM

large fragments were not perceived as better habitats than small ones.

Differences in nest success in relation to fragment size have been reported, but there is no consistent pattern. Some studies confirmed the generally expected negative relationships between fragment size and nest failure rate/nest predation (Møller 1991; Donovan et al. 1995; Hoover et al. 1995; Burke and Nol 2000; Luck 2003; Horn et al. 2005). Others, however, either detected no difference (Tewksbury et al. 1998; Friesen et al. 1999; Huhta and Jokimaki 2001; Mazgajski and Rejt 2006; Cooper et al. 2002) or even found positive associations (Zanette 2000; Brooker and Brooker 2001). In our study, overall nest failure rates and nest loss rates due to predation alone, respectively, were not related to fragment size either in the egg stage or in the nestling stage. This result is surprising because we had previously found that nests located in small old reed patches within wetland fragments were more likely to be predated than nests located in large patches (Pasinelli and Schiegg 2006) and that old reed area was positively related to wetland fragment size (see Methods). On the other hand, Pasinelli and Schiegg (2006) also failed to find effects at the scale of fragments, which is consistent with the findings reported here. It thus seems that nest failure in our study system is primarily mediated through effects acting at the scale of old reed patches within fragments (Pasinelli and Schiegg 2006) rather than at the scale of the wetland fragments (this study).

Compared to small fragments, large fragments have been shown to be associated with increased fledgling production (Møller 1991; Porneluzi et al. 1993; Donovan et al. 1995; Powell and Collier 1998; Luck 2003; Mazgajski and Rejt 2006) or fledgling mass (Burke and Nol 2000; Zanette et al. 2000; Loman 2003). Alternatively, increased reproductive success in small as compared to large fragments has been reported by Smith et al. (1996), Zanette (2001) and Brooker and Brooker (2001). Finally, no relationships between fragment size and either fledging success or fledgling weight were found by Tjernberg et al. (1993), Matthysen and Adriaensen (1998), Nour et al. (1998), Huhta and Jokimaki (2001) and Cooper et al. (2002). Our results are in line with the latter studies: fragment size alone did not explain much of the variation in either fledgling numbers or quality, but there was evidence for a fragment size by year interaction on fledgling numbers. Specifically, more fledglings per territory were produced in small fragments than in large fragments in 2004, but not in the other 3 years of the study. The same was true in terms of absolute number of fledglings produced in 2004: 72 fledglings originated from the small fragments ($n = 15$ territories), but only 51 fledglings from the three large fragments ($n = 23$). That fledgling production was so low in large fragments in 2004 may be related to the strong rainfall in June 2004, causing water levels of lakes in the three large fragments to increase by up to 0.5 m above normal levels. These high water levels extended several hundred meters inland and also destroyed nests of reed buntings outside old reed habitats. The flood was much less dramatic in small fragments, perhaps because only three fragments border a lake or large pond, and water receded much faster there than in large fragments.

Quality of fledglings was not associated with fragment size. This may be explained by the lack of a relation

between fragment size and arthropod biomass per unit area (Silvestri 2006), suggesting that large fragments were not more profitable feeding grounds than small fragments. Similarly, Møller (1991) did not find differences in food availability between small and large fragments. In contrast, Burke and Nol (1998) and Zanette et al. (2000) found food supply to be reduced in small compared to large fragments.

The relation between recruitment probability and fragment size is not well understood in birds because studies simultaneously examining the reproduction and recruitment of marked individuals over several fragments and years are rare. In fact, the only study found following an intensive literature search was the one by Matthysen and Adriaensen (1998), who reported the lack of a relation between recruitment probability and forest fragment size. In our study, territories in large fragments were not more likely to produce recruits than territories in small fragments, and vice versa. Further, relative to the numbers of fledglings produced, the combined number of recruits from the three large fragments (Greifensee, Lützelsee, Pfäffikersee, Table S1 in the ESM; 41 recruits out of 292 fledglings) was not significantly different from the combined number of recruits from all of the small fragments (15 recruits out of 164 fledglings; Yates-corrected $\chi^2 = 1.9$, $df = 1$, $P = 0.168$). Taken together, these findings again suggest that small fragments are valuable breeding sites for reed buntings because they appear to be equal to large fragments in contributing individuals to other fragments.

That we did not find improvements in reproductive performance and recruitment probability with increasing wetland fragment size could be due to small fragments offering higher quality habitats than large fragments, thereby offsetting the negative effects generally associated with small fragments. However, we consider this an unlikely explanation for the lack of relationships observed here. First, large fragments are generally assumed to offer higher quality habitats than small fragments because large fragments have maintained larger continuous tracts of the original habitat and thus suffer less from edge effects and other adverse influences of the matrix than small fragments. Second, in our study system, there were no relations between either wetland fragment size and arthropod diversity or arthropod biomass nor between reproductive success of reed buntings and arthropod biomass (Silvestri 2006). Moreover, home ranges of reed buntings did not differ in small and large fragments (O. Rickenbach, unpublished data). Finally, we found no significant relationships between fragment size and factors previously shown to affect nest success in the reed bunting (Pasinelli and Schiegg 2006), which likely reflect nest habitat quality (see Methods). Collectively, these findings suggest that habitat quality in terms of food availability and nest site characteristics did not differ among our study fragments.

The effects of the matrix on processes in fragments have been documented in recent years (e.g. Ricketts 2001; Debinski 2006). We did not include the composition of the landscape surrounding the fragments into our analyses because agricultural lands consisting mostly of intensively used meadows, cow pastures and crops (mostly corn) surrounded all fragments to a similar extent. Such habitats lack the prey species favored by the reed bunting. Furthermore, no effects of landscape composition on reed bunting reproduction in one of the 4 years were found (Bachmann 2005). Finally, radio-tracked reed buntings did not leave the wetlands in search for food (Silvestri 2006). These findings as well as our results suggest that matrix effects on reproduction were unlikely in the studied wetlands.

Since the sample sizes from small fragments were low, our analyses may lack the power to detect relationships between fragment size and reproductive performance. However, analysis of our data with small and large fragments pooled into two categories (small versus large) corroborated the findings presented here (data not shown), suggesting that a lack of power may not be of concern. Low sample sizes are an unavoidable consequence when studying systems mainly consisting of small fragments and local populations.

Local density

Although several studies have examined the relation between fragment size and reproductive performance, the effect of population density on reproduction has rarely been assessed simultaneously with fragment size. This is surprising since population density has been shown to influence different components of avian reproductive performance in various ways (e.g. Newton 1998). However, the commonly expected decrease in reproductive performance with increasing density has not always been confirmed. For example, in terms of laying date, several studies failed to find any effects of density on laying date (Wiktander et al. 2001; Arriero et al. 2006; Smith et al. 2006). Alternatively, the evidence for negative density-dependent nest success (Newton 1998; Müller et al. 2005) and fledgling production (Poysa and Pesonen 2003; Smith et al. 2006; Mallord et al. 2007) is strong; yet again, these relations have not always been found (Stenning et al. 1988; Vickery et al. 1992; Both and Visser 2003). Finally, density-dependent recruitment appears to be common in many bird species (Newton 1998).

We found no evidence for density-dependent reproductive performance or recruitment probability. The relation between density and reproduction may depend on the territorial system of a species and the resources defended (Both and Visser 2003): species having large, contiguous territories and competing mainly for food (a divisible resource) should show density-dependent reproduction, while species

with small territories that only defend nest sites (a non-divisible resource), should mostly show density-independent reproduction. Our findings are in line with the latter prediction because reed buntings defend small nest territories, but forage in non-defended areas outside their nest territories.

Alternatively, our measure of local density may not have accurately captured the possible effects of density, which may explain why we failed to find density-dependent reproduction. We believe, however, that the measure of local density used here better reflects intraspecific influences than the commonly used density estimate of number of breeding pairs in relation to the size of the study area. First, nest territories of reed buntings in our study fragments are often linearly arranged in areas of old reed, which border lakes or ponds, and the influence of birds from distantly located territories on a given territory is questionable. Secondly, although old reed areas are important for reed buntings when they settle in early spring (Glutz von Blotzheim and Bauer 1997; Surmacki 2004), it is not clear what an adequate representation of "area" would be to use as the denominator because the birds also need unknown amounts of space outside old reed areas to forage. The use of the extent of old reed as a representative of "area" can lead to unrealistically high densities, particularly in small wetland fragments, which only have very small old reed areas left.

Conservation implications

Reproductive performance and recruitment probability of reed buntings were not related to wetland fragment size, indicating that large and small fragments are equally suited as breeding grounds for this habitat specialist and should thus be managed to provide habitat for reed buntings, which may also be beneficial to other species dependent on old reed areas. Large fragments are important components of the reed bunting population network simply because of the large absolute numbers of breeding pairs. In turn, because a substantial percentage of all reed bunting pairs in our study area breed in large wetland fragments, reproductive failure in these fragments due to flooding may have a much stronger impact on regional population dynamics than comparable events in small fragments, and large fragments may act as sinks in flood years. Small fragments may thus help buffering negative effects of temporal variation in habitat conditions and so increase the persistence of spatially structured systems.

Finally, global change models generally predict increasingly wet winter/springs in temperate regions of the planet (Watkinson et al. 2004), which may lead to more numerous and perhaps more severe floods during the reproductive period in the future than has occurred in the past. The importance of small fragments may therefore even increase in the future, if large and small fragments continue to be differently affected by floods.

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